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Look where you're going! Perceptual attention constrains the online guidance of action

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Abstract

Action guidance, like perceptual discrimination, requires selective attention. Perception is enhanced at the target of a reaching movement, but it is not known whether selecting an object for perception reciprocally prioritises it for action. Two theoretical frameworks, the premotor theory and the Visual Attention Model, predict that this reciprocal relation should hold. We tested the influence of perceptual attention on the online control of reaching. In Experiment 1, participants attended covertly to a flanker on one or other side of a fixated target, prior to reaching for that target, which occasionally jumped, after reach onset, to the attended or non-attended side. Participants corrected their reaches for almost all target jumps. In Experiment 2, we required covert monitoring of the flanker *during* reaching. This *concurrent* perceptual task globally reduced correction behaviour, indicating that perception and action share a common attentional resource. Corrections were especially unlikely toward the attended side. This is explained by assuming that perceptual attention primed an action toward the attended location and that the participant inhibited this primed action. The data thus imply that perceptual selection constrains online action guidance, as predicted by the premotor theory and the VAM. We further argue that the fact that participants can inhibit a location within the action system but *simultaneously* maintain its prioritisation for perceptual monitoring, is easier to reconcile with the VAM than with the premotor theory.

1. Introduction

To support apt and skilful action, our visual systems must prioritise, specifying the spatial properties of goal objects and other relevant locations, and filtering out irrelevant information. Action guidance, like perceptual discrimination, requires selective visual attention (Allport, 1987). Because our visual experience feels unitary, we might naturally assume that we base our actions upon our explicit perceptions. But contemporary cognitive neuroscience suggests that this subjective unity is an illusion. There is extensive evidence for two broadly separate visual processing streams in the human brain: a ventral stream specialised for object recognition, and closely associated with perceptual awareness, and a dorsal stream optimised for the real-time guidance of action (Goodale & Milner, 1992; Milner & Goodale, 1995). A question that arises is whether vision-for-perception and vision-for-action depend upon shared or separable mechanisms of selective attention. That is, what is the relationship between *selection-for-perception* (SfP) and *selection-for action* (SfA)?

These functions cannot be entirely separate. Any object foveated for perceptual recognition, or as a target for action, will be processed within central vision, making higher acuity information about that object available for all behavioural purposes. But it is also possible to shift visual attention without movements of the eyes, providing possible scope for selection of different objects within different visual sub-systems. Milner and Goodale (1995) tentatively suggested an asymmetrical scheme, in which SfA determines the allocation of perceptual attention, but SfP does not reciprocally constrain action guidance (see also McIntosh, Schindler, Birchall, & Milner, 2005; Milner, 1995). Other theories have proposed tighter relationships, the tightest being the unity implied by the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). This influential theory proposes that spatial attention is instantiated within the pragmatic maps of the motor system, such that the planning of a goal-directed action (e.g. eye or hand movement) is both necessary and sufficient for a shift of visual attention to that location. That is, to attend visually to an object, we must plan a visually-guided action toward it, regardless of whether we subsequently execute that action, and the target of any such action will concurrently receive enhanced processing by the perceptual system. By the premotor theory, SfP and SfA should always co-occur, because they are one and the same.

A further scheme has been advocated by Schneider, Deubel and colleagues across several empirical papers (e.g. Deubel, Schneider, & Paprotta, 1998; Deubel & Schneider,

1996; Schneider & Deubel, 2002), and forms one aspect of a broader neuro-cognitive Visual Attention Model (VAM, Schneider, 1995). The VAM proposes that vision-for-perception and vision-for-action share a selection mechanism, operating on early visual representations prior to the split between ventral and dorsal streams. Selection involves the chunking of these early representations to define an 'object token' corresponding to the target. The creation of this object token has the consequence that the object's perceptual features are prioritised for processing in the perceptual recognition pathway, whilst information about its location and spatial features is forwarded to the action pathway to generate a candidate motor response. In this scheme, the distinction between SfP and SfA relates merely to the behavioural motive for which an object is selected. The mechanism of selection is the same in either case, and the consequence is that the target is prioritised for perceptual processing, and simultaneously primes a motor response, which may or may not subsequently be executed.

As noted by Schneider and Deubel (2002), the VAM assumes that motor programming is a downstream consequence of visual attention, where the premotor theory implies that visual attention follows from motor programming¹. This difference of detail will provide an important point of leverage to distinguish the theories with respect to our data in the Discussion. For present purposes, however, we emphasise the broader similarity between the two theories. Both predict that SfP should entail SfA and vice versa, and this prediction contrasts sharply with Milner and Goodale's idea that action guidance can be independent of perceptual attention (Milner, 1995; Milner and Goodale, 1995).

Many experiments have tested the impact of planning an action upon perceptual discriminations. In a now-classic experiment by Deubel and Schneider (1996), participants were centrally cued to perform a saccade to one of six lateralised locations, and were also required to report the identity of a probe, flashed at one of these locations during saccade preparation. Perceptual discrimination was enhanced selectively at the intended endpoint of the saccade, whilst remaining at chance levels even for immediately adjacent locations (1.5° distant). This yoking of SfP to SfA holds for manual actions such as reaching (Deubel et al., 1998; Baldauf, Wolf, & Deubel, 2006) and grasping (Castiello, 1996; Schiegg, Deubel, &

¹ In a recent review article, Smith and Schenk (2012) represented the VAM as a model specifically of SfA, which "*proposes that covert attention is a necessary precondition for goal-directed movement preparation, but makes no assumptions about the involvement of the motor system in covert attention when goal-directed actions are not required*" (p. 1108). This may be a mis-reading of the original VAM, which in fact suggests that covert visual attention to an object will automatically prime actions toward it, whether or not the task requires goal-directed action (Schneider, 1995). The reading of the VAM that we adopt above has been confirmed as valid by the model's originator, Werner Schneider (personal communication, 4 March 2014).

Schneider, 2003). However, for delayed actions, in which the action target is known in advance, the mandatory yoking of SfP to SfA relaxes for manual actions, but remains strong for eye movements (Deubel & Schneider, 2003). It may be that predictable hand movements can be configured in advance and subsequently executed 'offline', without concurrent selection of the target, but that eye-movements, even delayed ones, always involve online SfA. This capacity for 'offline' manual responses may be one factor to explain some outlying null results. Bonfiglioli, Duncan, and Rorden (2002) found no perceptual enhancement at the target of a reaching movement when the hand and target were hidden, so that the reach was cued from memory rather than selected online.

So, the preparation of action influences the distribution of attention in perceptual tasks. Note that this has been established using tasks, like that of Deubel & Schneider (1996), in which the action target is selected endogenously, without any visual transient at that location. Under these conditions, any associated enhancement of perceptual discrimination can be interpreted as an effect of SfA upon SfP. This interpretation, however, would be less secure if the action were cued by a sudden-onset target; any enhanced SfP at the action target could then be explained by the exogenous effects of the target signal, rather than by the endogenous intention to act. This is vital to appreciate because, when we consider the converse question of the effect of SfP upon SfA, we find that almost no studies have framed the issue in a comparable manner. Instead, researchers have studied the effect of exogenous attention, such as sudden-onset visual distractors upon different aspects of action guidance. Such studies do not speak directly to the effect of SfP upon SfA, but they are nonetheless worth discussing, because they indicate the sorts of effects of attention on action that we might expect to see.

When a visual distractor competes (unsuccessfully) as a saccade target, this may be revealed as a bowing of the trajectory toward the distractor (e.g. McPeck, Skavenski, & Nakayama, 2000; McPeck & Keller, 2001), or away from it (Doyle & Walker, 2001; Godijn & Theeuwes, 2002, 2004; Ludwig & Gilchrist, 2003; McSorley, Haggard, & Walker, 2004). Similarly, manual reach trajectories can veer toward (e.g. Chang & Abrams, 2004; Chieffi, Ricci, & Carlomagno, 2001; Grierson & Elliott, 2008; Song & Nakayama, 2008; Tipper, Howard, & Jackson, 1997; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999) or away from a salient cue or distractor (e.g. Gangitano, Daprati, & Gentilucci, 1998; Howard & Tipper, 1997; Tipper et al., 1997). These opposite patterns, of attraction and repulsion, can both be explained by proposing that the distractor initially primes an action response, producing attraction, but that top-down processes can inhibit that plan, producing repulsion

(Tipper, Howard, & Houghton, 1998, 2000; Van der Stigchel & Theeuwes, 2006). Whether trajectories deviate toward or away from the distractor is thus determined by how much scope there is for top-down factors to inhibit primed responses toward it. Accordingly, veering is sensitive to task variables such as preparation time and prior knowledge (Laidlaw & Kingstone, 2010; McSorley, Haggard, & Walker, 2006; Van der Stigchel & Theeuwes, 2005; Tipper, Howard & Houghton, 2000; Welsh & Elliott, 2004); participant capacity for top-down control may also be relevant, as pre-school children veer toward distractors from which adults veer away (Ambron, Della Sala, & McIntosh, 2012). However, for manual responses at least, attentional interference may be eliminated if the target location is known in advance, so that the reach can be pre-configured (McIntosh & Buonocore, 2012; Tipper et al., 1997).

As noted earlier, these effects of attention upon action, though interesting, do not show a specific effect of SfP on SfA. To test the specific effect of SfP requires attention to be allocated endogenously for perceptual discrimination, ideally when no visual change occurs that could bias SfA by an exogenous route. For instance, in Experiment 3 of Sheliga, Riggio, & Rizzolatti (1995), participants fixated a central symbolic cue that instructed them to attend covertly to one of four boxes, arranged in a square around fixation. The attended box contained a symbol that indicated whether a saccade should be made to an upper or lower target, vertically above or below fixation. All stimuli were on-screen from the beginning of the trial, so the shift of attention to the attended box was endogenous, and made solely to discriminate the symbol therein. Nonetheless, the attention shift induced a contralateral deviation in the trajectory of the ensuing saccade to the target. If we accept this deviation as evidence that a saccade to the attended box was primed and subsequently inhibited, then Sheliga's result indicates that SfP does indeed recruit SfA within the saccadic system.

The present study aims to test whether SfP similarly influences SfA during the online control of reaching. Online control is an important test case because it is probably the least disputed instance of a 'pure' dorsal stream function that might operate independently of the perceptual pathway (Glover, 2004; Rossetti, Pisella, & Vighetto, 2003; Schenk & McIntosh, 2010). For instance, Milner and Goodale (2008) have suggested that target selection for action may involve perceptual selection, but that online control is an autonomous function of the visuomotor system. Online control is typically studied using double-step tasks in which the target is jumped to a new location during a reach. Compensatory corrections are sufficiently rapid to be pre-conscious (Castiello, Paulignan, & Jeannerod, 1991), and occur even when participants are asked to react to target jumps in some other way, for instance by

stopping the movement (Pisella et al., 2000) or diverting it in the opposite direction (Day & Lyon, 2000; Johnson, Van Beers, & Haggard, 2002). Corrections are unimpaired by concurrent performance of a cognitively demanding auditory n-back task, further underlining their automatic nature (McIntosh, Mulroue, & Brockmole, 2010). Automatic correction has even been observed in the context of visual extinction, a pathological attentional imbalance, causing perceptual unawareness of the visual feedback on which the corrections are based, which suggests that online control is independent of perceptual attention (Schenk, Schindler, McIntosh, & Milner, 2005).

Liu, Chua and Enns (2008) have claimed to show that online control is similarly independent of SfP in the normal brain. These authors presented participants with a dual task, requiring them to monitor a rapidly changing stream of digits at fixation in order to identify a letter embedded amongst them, and simultaneously to point to a peripheral visual target, which would either remain still or jump by 10 mm after movement onset. In their single task condition, the same stimuli were presented, but letter identification was not required. The perceptual dual task retarded movement initiation, suggesting an effect of perceptual attention on initial target selection, but the authors found no effect of the dual task upon pointing accuracy in either jump or no-jump trials. However, this is rather weak evidence for independence between SfP and SfA during online control. First, Liu et al's perceptual task did not just involve endogenous attention, but used a rapidly changing stream of digits, which would attract attention exogenously, regardless of whether the participant was instructed to monitor it. The freedom for SfA to be allocated differently between single and dual task conditions may thus have been limited. Moreover, the perceptual task, performed in central vision, seems to have been very easy, with letter identifications above 95% correct, so may have left sufficient spare attentional capacity to support adequate online control in the periphery, even in the dual task condition. Contrary to Liu et al, a study of reach-to-grasp behaviour, using a similar rapid serial visual identification task, but with prior adjustment of stimulus size and durations to ensure below-ceiling performance, did show dual-task interference with movement initiation and with grip formation as the hand approached the target (Hesse & Deubel, 2011). Hesse and Deubel interpreted this as demonstrating co-dependence of SfP and SfA during both movement planning and online control. However, since they did not perturb the action target in any way after reach initiation, there was no direct demonstration of perceptual interference with online control (see also Hesse, Schenk & Deubel, 2012).

In the present study, we aim to test specifically whether SfP constrains SfA during the online control of reaching. In two experiments, we manipulate the location to which perceptual resources are endogenously allocated, and study movement corrections when the reach target jumps to the same or opposite side of space. Thus, we use an exogenous visual probe (the target jump) to measure visuomotor responsiveness (SfA) to each side, as a function of endogenous perceptual attention (SfP). In Experiment 1, we vary the location of SfP immediately prior to reaching; in Experiment 2, we constrain SfP *during* the reach. If online guidance of action is independent of perceptual processing (Liu et al, 2008; Milner, 1995; Milner & Goodale, 1995), then corrections should be unaffected. By contrast, both the VAM (Schneider, 1995) and the premotor theory of attention (Rizzolatti et al, 1987) predict that SfP will affect the likelihood and/or the extent of online correction. The *direction* of effect is less easy to predict, given that facilitatory and inhibitory influences of attention on action have been reported in previous work. However, the facilitatory or inhibitory nature of the effect may, as we shall argue, further discriminate between the VAM and the premotor theory.

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2. Methods

2.1. Participants

Twelve participants (8 women, mean age = 22 years, SD = 2.73) took part in Experiment 1, and twelve different participants took part in Experiment 2 (8 women, mean age = 21.67 years, SD = 2.57 years) for £6 payment. All were right-handed by self-report and had normal or corrected to normal vision. This study was approved by the Psychology Research Ethics Committee, University of Edinburgh.

2.2. General set-up (Figure 1)

Participants were seated in a darkened room with their head stabilised by the chin rest of an Eyelink 1000 (SR Research, Osgoode, Canada) video-based eye tracker. Stimuli were presented on a 21" screen (400 x 300 mm active display, 1024 x 768 resolution, 100 Hz refresh) suspended face-down above a front-surface mirror via which the participants viewed them. The stimuli appeared optically to be on a slightly inclined working surface at the level of the participant's hand. The mirror was midway between the monitor and this working surface, preserving the optical sizes of the stimuli. The central target was 12 mm in diameter, and appeared to the participant to be 400 mm in front of the start button that their right index finger depressed at the start of each trial. Flanker stimulus locations were 75 mm to left and right of the central target. The display background was black, and all stimuli were white except where stated. Trials were always shuffled randomly. The mirror arrangement meant the hand was not visible to the participant. This aspect of the design was to ensure that there were no visual transients from the hand that could exogenously disrupt attentional allocation.

The Eyelink was used to monitor fixation, and trials were interrupted if the eye moved more than 30 pixels ($\sim 1.13^\circ$) from the central target prior to button release. A 5-point horizontal-vertical calibration was carried out at the start of the experiment and repeated as necessary, and drift correction was performed at the start of each trial. The Eyelink sampling rate was 1000 Hz. Pointing movements were monitored by attaching to the participant's right index fingernail an infrared emitting diode (IRED), which had its 3D location sampled by the Optotrak Certus system (Northern Digital Inc., Waterloo, Canada) at a rate of 100 Hz. The Optotrak was registered to the workspace, such that the start button was at the origin of a Cartesian coordinate system, and lay in the same XY plane as the targets so that the targets

were at 400 mm on the Y-axis, with the central target at zero on the X-axis, and the two flanker locations at -75 and 75 mm (see aerial view of workspace in Figure 4a).

2.3 Experiment 1 – SfP prior to reaching (Figure 2a)

In Experiment 1, we required participants to attend covertly to one or other side of the central target dot, immediately prior to initiating a fast reaching movement. The initial display contained a flanking asterisk (12 mm diameter) on either side; the participant was required to fixate the central target but to monitor one or other asterisk for a change to a plus or a cross (by offset of the diagonal or the horizontal/vertical arms respectively). A cross signalled a NOGO-trial, in which the participant had to refrain from responding until the end of the trial 1000 ms later; NOGO trials were included to ensure that participants were accurately performing the required perceptual discrimination. A plus signalled a GO-trial, in which the participant had to make a rapid reach to the central target. On a subset of GO-trials, the target dot jumped either to the left or the right flanker position, thus either to the attended or non-attended side. The side to which participants were instructed to attend was manipulated on a block-by-block basis.

The participant was familiarised with the basic reaching task via a practice block of 45 trials. Practice trials were similar to subsequent experimental GO-trials, except that they did not require specific monitoring of one or other flanker location, allowing the participant to concentrate instead on the reaching demand. Each practice trial began with the participant fixating the central target and depressing the start button. After a delay that varied randomly between 750-1500 ms, both asterisks turned to plus signs, and the participant had to make a fast reach to the central target. On 15 trials, the target remained at the centre, on 15 trials it jumped to the left flanker position, and on 15 trials it jumped to the right flanker position immediately after button release. Any trial in which the participant released the start button before the flanker change, or moved the eyes from the centre before button release, was reshuffled. If participants did not initiate their reach within 750 ms of the flanker change on GO-trials, the words “Too Slow” appeared, accompanied by an error tone, and the trial was reshuffled. To encourage rapid reaches, a high pacing beep sounded 350 ms after button release, and participants were asked to try to complete their movements by the time of the beep. Participants were instructed to leave their hand in its landing position until the

target disappeared, 650 ms after button-release. The display was then replaced by the message “Press for next trial”, and the participant returned the hand to the start button.

Following practice, each participant completed four blocks of experimental trials. These were similar to practice trials, except that in each block the participant was required to respond as instructed by the symbol that replaced the asterisk on one or other side, thus to reach if this was a plus (GO-trial), but not if it was a cross (NOGO-trial); the unattended asterisk simultaneously turned to a cross or a plus, but the symbol was perfectly uncorrelated with the symbol on the attended side. Each experimental block consisted of 50 experimental trials preceded by 15 practice trials drawn randomly from the trial sequence. The 50 experimental trials comprised 32 GO trials (20 target no-jump, six jump-left and six jump-right) and 18 NOGO-trials. If participants released the start button on NOGO-trials, they received an error tone and the on-screen message, "NO-GO Trial: Keep finger on button", but these trials were not reshuffled. The attended side was blocked according to an ABAB schedule, beginning with the left side for half the participants. Across the four blocks, participants thus completed 40 no-jump, 12 jump-left, 12 jump-right, and 36 NOGO trials per attended side.

Experiment 1 manipulated which side of space was endogenously attended, for the purposes of perceptual discrimination, immediately prior to reach initiation. This was not a ‘pure’ manipulation of SfP, since there were exogenous transients associated with the changing of the asterisks. However, these changes were visual offsets, which are of relatively low salience to visual attention (Cole, Kentridge, Gellatly, & Heywood, 2003) and, crucially, the asterisks on both sides of space always changed simultaneously, so that this exogenous component was spatially balanced. Any lateralised effects on correction behaviour should therefore be interpretable as due to the instructed allocation of SfP.

2.4 Experiment 2 – SfP during reaching (Figure 2b)

In Experiment 2, we tied the SfP demand more closely in time to the reaching task, so that participants had to monitor the flanker continuously on one or other side for a subtle flicker during the reach. The side to which participants were instructed to attend was manipulated on a block-by-block basis, and participants were informed that the flicker would only ever occur on the attended side, though they were not told how often to expect it. Our main kinematic

analyses were restricted to trials in which the flicker did not occur, so that we were able to study the consequences of attending endogenously to a location for perceptual discrimination, independently of that perceptual change occurring.

The basic trial sequence was similar to that of Experiment 1, except where indicated. At the start of each trial, the participant was required to fixate the central target and to depress the start button. The initial display contained a small (0.14°) mid-level grey square on either side. As soon as the participant felt ready, they were to reach rapidly for the central target and to monitor the grey square on one or other side for a flicker. On no-jump trials, the central target did not move; on half of these trials, the grey square on the attended side would flicker (i.e. disappear for 20 ms at button release); the square on the non-attended side never flickered. As in Experiment 1, rapid reaching movements were encouraged by a high pacing beep 350 ms after button release, and in Experiment 2 this was reinforced by the disappearance of the display after 350 ms. On no-jump trials, after a further 650 ms, the word “Flicker?” appeared in the centre of the screen, and the participant had to answer verbally “yes” or “no”, their response being keyed in by the experimenter. On jump trials, the grey squares never flickered, but the target jumped to the location of the grey square on one or other side immediately after button release. On jump trials, the end of trial screen simply presented the word “Ready?”, to which participants could respond verbally before initiating the next trial.

The participant was familiarised with the basic reaching task via a practice reaching block of 45 trials (15 no-jump, 15 jump-left, 15 jump-right), in which they were not instructed to monitor the grey dots. Next, they were familiarised with the basic perceptual task by performing two blocks of 20 no-jump trials, in which they monitored for a flicker on the left side in the first block, and on the right in the second, with the flicker occurring on one half of the trials in each practice perceptual block.

Following practice blocks, each participant performed four experimental blocks. Each experimental block consisted of 60 trials preceded by 10 practice trials drawn randomly from the trial sequence. The 60 experimental trials comprised 40 no-jump trials, half of which contained a flicker on the attended side, and ten jump trials to either side. The attended side was blocked according to an ABAB schedule, beginning with the left side for half the participants, and the right for the other half. Across the four blocks, participants thus

completed 60 no-jump trials with flicker, 60 no-jump trials with no flicker, 40 jump-left, and 40 jump-right trials per attended side.

2.5 Data processing and preliminary analyses

For Experiment 1, NOGO trials with saccades (11.1 % of trials) or where participants released the starting button (4.2 % of trials) were considered failed. For both experiments, trials with incomplete kinematic information due to marker occlusion were discarded (1.1 % of trials in Experiment 1, and 0.3 % of trials in Experiment 2). For the remaining trials, raw kinematic data were filtered by a dual pass through a Butterworth filter with a cut-off of 20 Hz. Movement onset was defined by button release, and movement offset was defined as the final frame before which the speed of movement fell below 50 mm/s.

For Experiment 1, the following movement variables were extracted: reaction time (RT) from cue onset to button release; movement time (MT) from movement onset to offset; peak speed (PS) of movement; time to peak speed (TPS) from movement onset; amplitude of movement (AMP) from the IRED's start position to its final position in the XY plane of the workspace; terminal angle (ANG) of the IRED's final position with respect to its start position in the XY plane of the workspace. We also calculated reach curvature (CURV), using a computation adapted from Appendix A of Van der Stigchel, Meeter, and Theeuwes (2006). First, we transformed each reaching movement so that the straight line path from the start to the end point was aligned with the Y-axis. We then spatially normalised each movement to 100 equally spaced increments along the Y-axis, and calculated the average X coordinate across the 100 samples, to produce a measure of average curvature in mm, where negative values represent leftward curvature and positive values rightward curvature. For Experiment 2, we extracted the same movement variables, except that RT was not relevant because the initiation of reaching was self-paced, and we additionally calculated the rate of correct flicker discrimination (DISCRIM) on no-jump trials.

For both experiments, our key dependent measure was Terminal Correction Rate (TCR) in jump trials. This is the percentage of trials that were deemed to be in a corrected position in the final frame of movement, by reference to reaching behaviour in no-jump trials. First, for each participant, for each attention condition, we grouped all no-jump trials, and calculated the mean and SD of the terminal angle (ANG). (For Experiment 2, no-jump trials

with a flicker event were excluded from this calculation.) For each jump trial, we coded terminal correction status as 1 (i.e. corrected) if ANG fell more than 2.81 SDs from the no-jump mean, *in the direction of the jump*, and as zero if it did not. Each comparison thus approximates a one-tailed comparison at alpha 0.0025. This alpha was chosen, somewhat arbitrarily, to constrain type I error rate to 5% across the 20 jump trials per block in Experiment 2, and for consistency with prior studies in our group (e.g. McIntosh et al, 2010; McIntosh, Mulroue, Blangero, Pisella & Rossetti, 2011); the same criterion was applied in Experiment 1 for cross-comparability between experiments. TCR was simply the average correction status multiplied by 100.

3. Results

3.1 Experiment 1 – SfP prior to reaching

A preliminary analysis was conducted for Experiment 1 to compare RTs between GO trials in which the unattended flanker was either congruent (plus) or incongruent (cross) with the attended flanker. Any influence of flanker congruence would indicate that participants were not able to attend exclusively to a single flanker location. For each participant, median RT was extracted for congruent and for incongruent GO trials separately for each side of attention (left, right); jump and no-jump trials were pooled for this analysis, because RT is measured prior to the target jump. A repeated-measures ANOVA by attention side and flanker congruence found no significant effects; average RT was closely similar between congruent and incongruent trials (499 vs. 501 ms; $p = 0.72$). Along with the low rate of reaching responses on NOGO trials (4.2 %), this provides reassurance that participants were attending effectively to the instructed flanker.

The rates of terminal correction in jump trials were overall high. Indeed, they were at ceiling for 22 out of the 48 combinations of participant by condition. Given these ceiling effects, non-parametric analyses were used for this variable. A boxplot of median TCR for each condition is shown in Figure 3a. In order to formally analyse the effect of SfP, the data for each participant were collapsed to two conditions, by taking the mean of the medians for jump trials to the attended side (mean of jump-left, attend-left and jump-right, attend-right) and the non-attended side (mean of jump-left, attend-right and jump-right, attend-left). A Wilcoxon signed rank test found no significant difference [$Z = 0.62$, $p = 0.53$], providing no indication that correction behaviour was either boosted or blunted toward the attended side.

For additional analyses of movement variables, the relatively few uncorrected jump trials were excluded. For descriptive purposes, we calculated the median movement endpoint in the X and Y dimensions for each participant in each target condition, and the group means of these values are shown in Figure 4a. Generally, participants reached short of the target, most so the left target, and least so for the right target. Two factors may have promoted this tendency. First, the task was performed without vision of the hand, or tactile feedback from targets, so visual-proprioceptive calibration of the working space was not possible. Second, the start button was 253 mm in front of the participant, and the target was 400 mm more distant, which was close to full stretch for some people. Participants might thus have tended to scale their reaches to their own comfortable reach distance, which would tend to be farthest

on the right (ipsilateral) side, and least far on the left. Individually, whilst four participants reached on average further than the target (the farthest average reach for the middle target was 432 mm), the rest reached less than 350 mm. Figure 4b shows sample trajectories for the participant with the shortest average reach, illustrating that, although the reaches were systematically short in the depth dimension, they were appropriately related to the horizontal position of the target, with movement corrections to the left and right locations emerging smoothly during the course of the reach.

In order to probe further for effects of side of attention, analyses of movement variables were conducted for no-jump and corrected jump trials. For each participant, median values were extracted for AMP, ANG, CURV, MT, PS and TPS, for each combination of attention side (left, right) and target location (left, middle and right). Medians were used as robust estimates of central tendency, per participant, as few corrected jump trials were sometimes available. The group patterns are shown in Figure 5. Separate repeated-measures ANOVAs found a significant effect of target location for every movement variable [all $F(2, 22) \geq 11.37$, $p < 0.005$, $\eta_p^2 \geq 0.50$], but no significant main effect of attention [all $F(1, 11) \leq 0.54$, $p \geq 0.47$], or interaction [all $F(2, 22) \leq 1.04$, $p \geq 0.36$]. The pattern of responding to different locations can be seen in Figure 5. Participants reached increasingly far for targets from left to right, consistent with a further comfortable stretch on the ipsilateral side. Because trajectory corrections toward the new target location unfolded during the reach (see examples in Figure 4b), corrected reaches had a rightward CURV for left targets and a leftward CURV for right targets. Corrected reaches, especially those to the left, had extended MTs; and reaches to the right tended to reach a higher peak speed at a later time. Formal post-hoc tests were not conducted, because no theoretically relevant effects of attention were involved.

Overall, then, Experiment 1 found no evidence for any influence of prior SfP upon immediately subsequent online correction. This result is, at best, inconclusive, because the task was rather easy for participants, and TCR was at ceiling in many cases, which could have obscured subtle effects of attention condition. Nonetheless, these generally high rates of correction will provide a useful baseline against which to compare performance during the more demanding concurrent SfP task introduced in Experiment 2.

3.2 Experiment 2 – SfP during reaching

Discrimination accuracy in the perceptual monitoring task of Experiment 2 was generally good, but well below ceiling (78% overall, where 50% is chance level, with no difference between flicker discrimination on the left and right: $t(11) = 0.71$, $p = 0.50$), confirming that participants attended to the monitoring task, and that it was a difficult one. Experiment 2 was designed for the reaching analyses to be restricted to no-flicker trials, in order to study the effects of SfP in the absence of any visual transient events preceding the target jump. Preliminary repeated-measures ANOVAs were conducted for each movement variable (median per condition per participant), to compare no-jump trials in which a flicker occurred against those in which it did not, with side of attention as an additional within-subjects factor. There were no significant effects involving side of attention, but flicker had a significant influence on MT [$F(1, 11) = 30.46$, $p < 0.0005$, $\eta^2_p = 0.74$] and on AMP [$F(1, 11) = 6.32$, $p < 0.05$, $\eta^2_p = 0.37$], with movements briefer (mean MT 374 vs 389 ms) and of correspondingly reduced amplitude (mean AMP 263.3 vs 267.8 mm) on flicker trials. These effects did not interact with the side of attention, so we interpret them as non-specific consequences of participants alerting to the flicker. These minor effects further justify the exclusion of flicker trials from other analyses.

The key measure, TCR, is represented as a boxplot in Figure 3b, for direct comparison to the corresponding data from Experiment 1 (Figure 3a). A Mann-Whitney test to compare the global correction rate (collapsed across conditions) between experiments confirmed a significant depression of TCR in Experiment 2 [$U = 27$, $p < 0.01$], indicating that the dual-task demand of lateralised visual monitoring reduced visuomotor responsiveness to the target jump. TCR data for Experiment 2 did not suffer ceiling effects, and are re-plotted parametrically in Figure 6c. A repeated measures ANOVA by jump side (left, right) and attention side (left, right) found a significant interaction, reflecting relatively lower rates of correction toward the attended side [$F(1, 11) = 16.41$, $p < 0.005$, $\eta^2_p = 0.60$]. The critical difference, between TCR for corrections to the attended and unattended side, is depicted in the right portion of Figure 6c.

Figure 6a shows a descriptive plot of the group mean of median movement endpoints for no-jump and corrected jump trials. As in Experiment 1, participants reached short of the true target location, most severely for the left target, and least so to the right target. For completeness, average endpoints of uncorrected jump trials are plotted in Figure 6b; but there

were generally low numbers of uncorrected trials (two participants had no uncorrected trials in at least one condition), and these trials were not analysed further. Analyses of movement variables were conducted for no-jump and corrected jump trials, exactly as for Experiment 1, and quite similar patterns were obtained (Figure 7). Separate repeated-measures ANOVAs found a significant effect of target location for every variable [all $F(2, 22) \geq 8.71$, $p < 0.01$, $\eta^2_p \geq 0.44$], except for PS. As before, the side of attention had no significant effect [all $F(1, 11) \leq 0.31$, $p \geq 0.59$] or interaction [all $F(2, 22) \leq 1.93$, $p \geq 0.18$] for any variable. This supplementary analysis of the kinematic character of reach corrections is not high-powered, given the limited numbers of jump trials available. However, it suggests that the effects of SfP are principally on the likelihood of making a correction to one or other side; these corrections, once initiated, unfold quite similarly, regardless of the location of SfP.

4. Discussion

Across two experiments, we investigated whether perceptual attention constrains the online control of reaching. In Experiment 1, perceptual discrimination immediately preceded the reaching task. In Experiment 2, the perceptual demand was concurrent with reach execution. We did not see effects of perceptual attention on no-jump trials, in which the reach target did not jump. This lack of influence on no-jump trials was expected, because every reach was directed initially to the same central target position, and highly predictable manual responses are often resistant to attentional distraction (McIntosh & Buonocore, 2012; Tipper et al., 1997). Instead, our interest was in the rates of online correction for reaches during which the target jumped toward or away from the attended side. According to Milner and Goodale (2008), the planning of a visually-guided reach may involve perceptual selection of the target but, once underway, its online control is an autonomous function of the visuomotor system. Thus, if SfA is dissociable from SfP, online correction is an ideal candidate behaviour in which to demonstrate the dissociation (Liu et al., 2008; Schenk et al., 2005).

Experiment 1 did not show any effect of prior SfP on online correction. Superficially, this suggests that online control can indeed dissociate from perceptual attention, consistent with the findings of Liu et al. (2008). However, Experiment 1 cannot be considered a strong test of the relation between SfP and SfA, because correction rates were at or close to ceiling level in all conditions. This confirms that online correction is highly efficient, but it provides scant basis for probing differences in correction efficiency between conditions. An alternative or additional explanation for the failure to find an influence of prior SfP in Experiment 1 might be that the perceptual task did not overlap in time with reach execution. This may have enabled the participant to perform the perceptual and visuomotor tasks in sequence, disengaging perceptual attention from the lateralised stimulus before initiating the reach. Nonetheless, Experiment 1 serves a useful purpose, because it demonstrates normally responsive online correction behaviour for the reaching stimuli used here, and thus provides a baseline against which to compare online correction rates in Experiment 2, in which the perceptual task did overlap in time with reach execution.

The first striking aspect of online correction rates in Experiment 2 was that they were globally depressed by comparison to Experiment 1, with only 58% of jump trials on average triggering corrections. This indicates that perceptual attention to a stimulus other than the initial reach target disrupts the ability to make online corrections. It is important to note that

this disruption was caused by the endogenous monitoring itself, not by the flicker event that was monitored for, as this never occurred in the jump trials in which corrections were studied. This refutes the conclusions of Liu et al. (2008), who reported no effect of a perceptual monitoring task on online reach correction. As noted in the Introduction, there may be at least two artefactual explanations for Liu et al.'s null finding. First, their perceptual stimulus involved exogenous visual changes, in both dual and single-task conditions, which may have tended to make attentional allocation similar between conditions. Second, and more crucially, their perceptual task was performed in central vision and was rather easy, with average accuracy higher than 95%, so may have spared sufficient attentional resources to support online correction. By contrast, our own perceptual monitoring task was presented away from fixation, and was performed with an average accuracy of 78% (where 50% is chance level), suggesting that it was much more challenging. This dual-task interference contrasts sharply with the finding that a highly demanding *auditory* task does not impair visually-based online reach corrections (McIntosh et al., 2010), implying that it is due specifically to the perceptual task loading on the same visual attention resource as online correction, and not to some more general attentional or executive resource limitation (see also Hesse & Deubel, 2011; Hesse et al., 2012).

The demonstration of global perceptual interference with online correction confirms a degree of dependence of SfA on SfP. But Experiment 2 additionally showed a specific directional influence of SfP, such that corrections were least likely to be directed to the monitored location, and *relatively* more likely to go to the opposite side. This inhibitory effect of attention is reminiscent of the trajectory deviations observed for reaching movements (e.g. Gangitano et al., 1998; Howard & Tipper, 1997; Tipper et al., 1997) and saccades (Doyle & Walker, 2001; Godijn & Theeuwes, 2004; Ludwig & Gilchrist, 2003; McSorley et al., 2004; Sheliga et al., 1995) under conditions in which top-down factors, such as distractor predictability, give participants scope to actively inhibit the distractor location. In Experiment 2, relevant top-down knowledge was *always* available, because participants were instructed which side to monitor for the perceptual change. Within a vector-based action coding framework, the inhibition effect can be taken as evidence that allocating SfP automatically primes an action to the attended location. In order to reach to the central target, the participant must actively inhibit the primed flanker location in the relevant motor map, and this inhibition is revealed by a reduced likelihood of online correction if the target

subsequently jumps to that location; though, once a correction is actually implemented, its kinematic character and extent does not much differ as a function of SfP.

When considered alongside prior literature showing that SfA constrains SfP, our findings indicate that the relationship is reciprocal: SfP constrains SfA, even for an automatic visuomotor behaviour such as online correction. Previous studies have shown biasing of manual responses away from attended locations, but these effects have always been interpretable as a suppression of the primed action plan once attention has left that location. Our Experiment 2 adds unique value in two ways: first, by showing inhibitory effects of a purely endogenous perceptual task on reaching, as previously done for the saccadic system by Sheliga and colleagues (1995); second, by showing that these effects can be *concurrent* with ongoing perceptual prioritisation of the same location. At first sight, a reciprocal yoking of attention between perception and action may seem equally consistent with the VAM (Schneider, 1995) and the premotor theory (Rizzolatti et al., 1987). On closer consideration, our particular findings may be problematic for the premotor theory. According to this theory, SfP is identical with SfA, depending directly upon activation within the same pragmatic maps, so to inhibit an action plan to any location would simultaneously prevent perceptual monitoring of that location. Without adding further assumptions, such as inhibition at motor output stages, the premotor theory cannot explain how our participants could suppress actions to a location, whilst simultaneously performing a difficult perceptual monitoring task there.

On the other hand, the VAM can accommodate these findings with relative ease, because this model does not assume any co-dependence of perceptual and motor representations beyond an initial shared mechanism of visual selection. According to the VAM, perceptual attention to the monitored location would initially prime action responses to the same location, because of this shared selection mechanism, but top-down inhibition could be applied subsequently to the primed location within the relevant pragmatic maps of the action system, without any parallel diminution of the corresponding perceptual representation. This flexibility within the VAM also makes it possible to imagine that awareness for one side of space could be impaired at a relatively late stage of perceptual processing, without compromising visuomotor responsiveness to the same locations, potentially allowing for neuropsychological dissociations of action from awareness (e.g. McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; McIntosh et al., 2005; Milner & McIntosh, 2005; Schenk et al., 2005).

The present experiments provide clear evidence that SfP constrains SfA during ongoing visually-guided action, consistent with evidence from Hesse and colleagues (Hesse & Deubel, 2011; Hesse et al, 2012), and refuting the idea of independent selection mechanisms for perception and action (Liu et al., 2008). Allocating attention endogenously for the purposes of perceptual monitoring grossly reduces online correction behaviour, and corrections are least likely to be triggered toward the attended location. This inhibition of action at the focus of perceptual attention echoes the known influence of exogenous distractors on reaching trajectories, and implies top-down inhibition of actions primed automatically toward the attended location. The priming and subsequent inhibition of actions to a location attended purely for perceptual discrimination is broadly consistent with both the VAM (Schneider, 1995) and the premotor theory (Rizzolatti et al., 1987). Crucially, however, the inhibition of corrections to the attended location that we observed was *concurrent* with successful perceptual monitoring at that location. This wholly novel pattern implies a high degree of independent control over action representations, subsequent to initial target selection, and favours the VAM over a premotor account.

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Figure legends

Figure 1: Schematic diagram of the set up (not to scale, chinrest not shown). Stimuli were presented on a monitor and optically projected via a mirror to an inclined working surface in front of the participant. Solid lines indicate critical components of the apparatus; dashed lines are included to indicate measurements, and dotted lines to assign labels.

Figure 2. (a) Experiment 1: schematic examples of the stimulus sequence for jump trials. In this example the participant initially fixates the central target, and attends covertly to the left flanking asterisk. After a random delay (750-1500 ms), this flanker turns into a plus sign, signalling for the participant to perform a pointing movement to the central target. At movement initiation, the central target jumps either to the attended side (left) or the non-attended side (right), and the participant must correct his or her movement online. **(b)** Experiment 2: schematic examples of the stimulus sequence for a no-jump trial with flicker (left branch) and a jump trial (right branch). The participant initially fixates the central target and attends covertly to the left flanking square. The reach is self-initiated, and the participant must monitor the attended flanker for a brief flicker at movement onset, which is present on half of no-jump trials. The flicker is a brief (20 ms) disappearance of the flanking square. Following the movement, the participant is asked to verbally report whether they detected a flicker. Jump trials were similar to Experiment 1, with the target jumping to one of the two flanking locations at button release. There is never a flicker on jump trials, and the participant must simply report when they are ready to begin the next trial.

Figure 3. (a) Experiment 1: the left section shows Terminal Correction Rate for the four combinations of jump side and attention side. The right section isolates the critical value for theoretical purposes, being the effect of side of attention (same or opposite side) on correction rate. Correction rates were subject to ceiling effects in Experiment 1, so box-plots are shown (horizontal lines are medians, boxes span 25th-75th percentiles, and whiskers span 10th-90th percentiles, with outliers shown). **(b)** Experiment 2: boxplot of Terminal Correction Rate, for comparability to Experiment 1 data in panel (a). An alternative, parametric plot of Experiment 2 Terminal Correction Rate is shown in Figure 6c.

Figure 4. (a) Experiment 1: aerial view of the workspace, showing average endpoints of the reaches made on no-jump and corrected jump trials, under the attend-left and attend-right conditions. Note that participants reached short of the true target positions, which are marked by the symbols at the top of the plots (circle is left target position, square is mid target

position and diamond is right target position). Average within-subject IQRs in lateral and depth dimensions are indicated by the length of the horizontal and vertical arms of the crosses below each target. **(b)** Exemplar trajectories for the participant with the shortest average reach. Although the reaches were systematically short in the depth dimension, they were appropriately related to the horizontal position of the target, with movement corrections to the left and right locations emerging smoothly during the course of the reach.

Figure 5. Experiment 1: average movement variables for no-jump and corrected jump trials. Error bars represent the average within-subject IQRs.

Figure 6. Experiment 2: aerial view of the workspace, showing average endpoints of the reaches made on no-jump and corrected jump trials, under the attend-left and attend-right conditions. Separate plots are shown for those jump trials that were classed as corrected **(a)** and as uncorrected **(b)**; the no-jump data are the same in panels (a) and (b). Note that participants reached substantially short of the true target positions, which are marked by the unfilled symbols at the top of the plots (circle is left target position, square is mid target position and diamond is right target position). The average within-subject IQRs in lateral and depth dimensions are indicated by the length of the horizontal and vertical arms of the crosses below each target. Panels (a) and (b) show that the side of attention had relatively little influence on the spatial extent of reach correction to the left or right. Panel **(c)** indicates that attention had a significant influence on whether a reach correction was made at all. The left section of panel (c) shows TCR in the four combinations of jump side and attention side; the right section isolates the effect of side of attention (same or opposite side) (\pm 95% CI), confirming a reduced rate of reach correction to the attended side.

Figure 7. Experiment 2: average movement variables for no-jump and corrected jump trials. Error bars represent the average within-subject IQRs.

Figure 1.

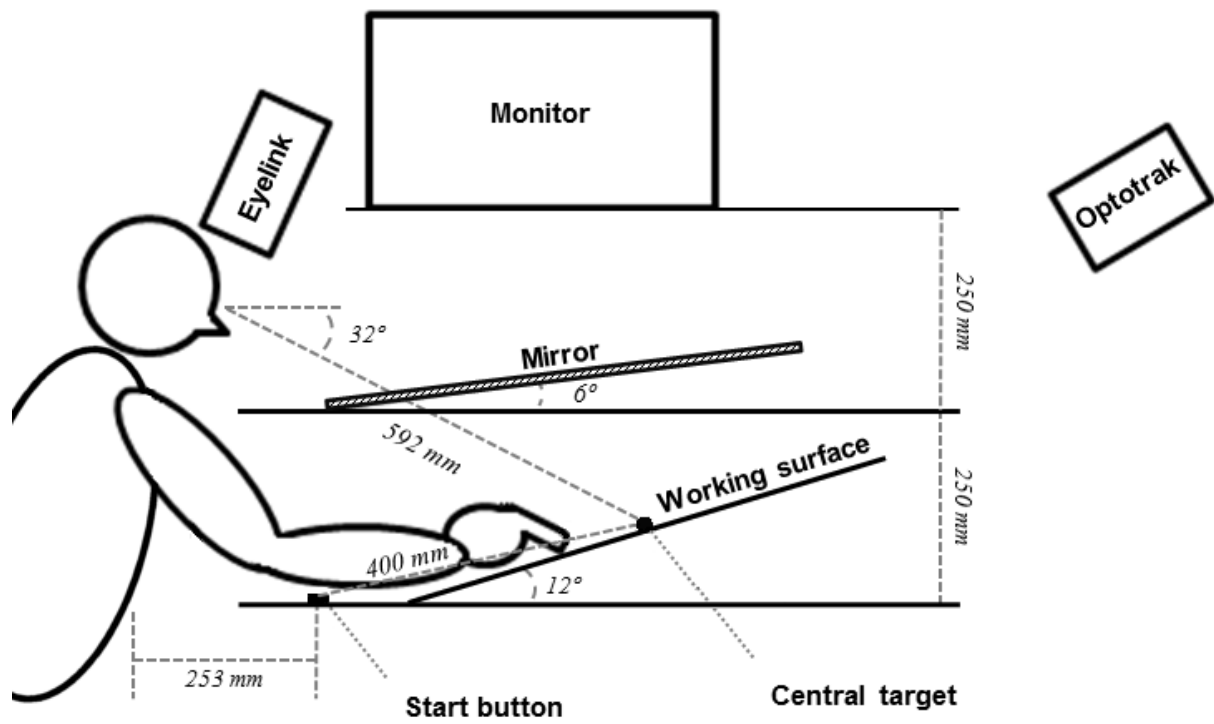
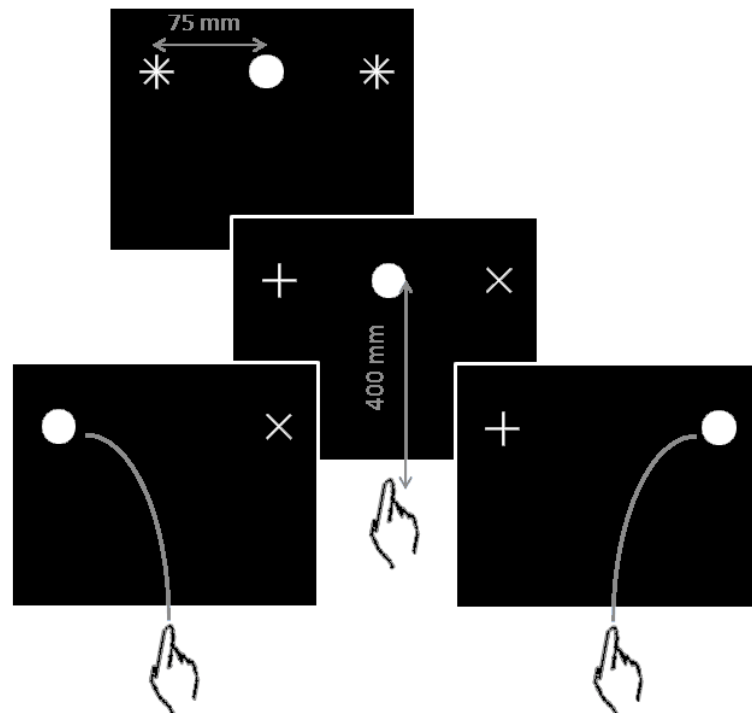


Figure 2.

(a)



(b)

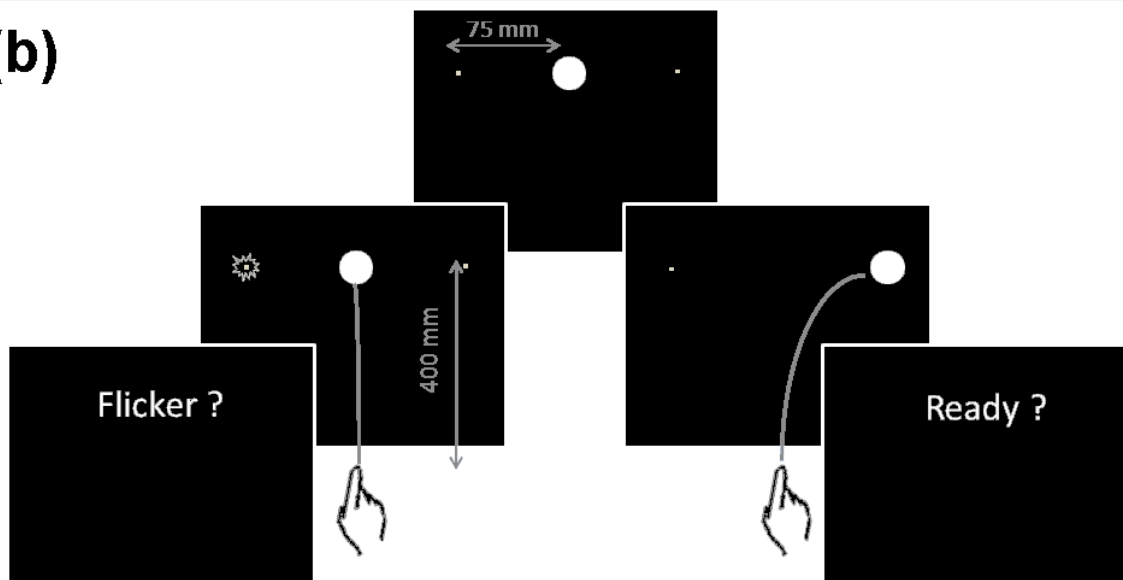


Figure 3

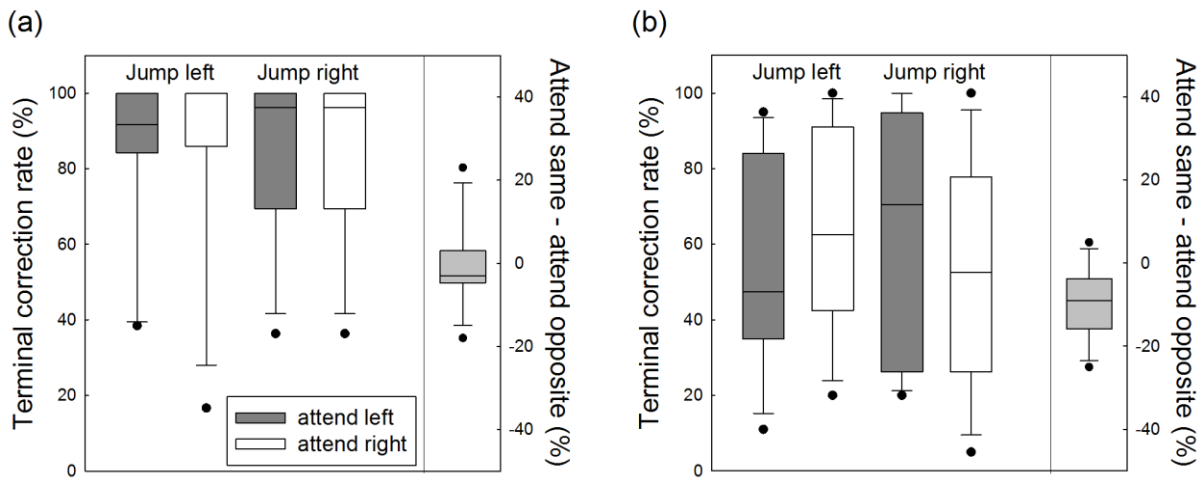


Figure 4.

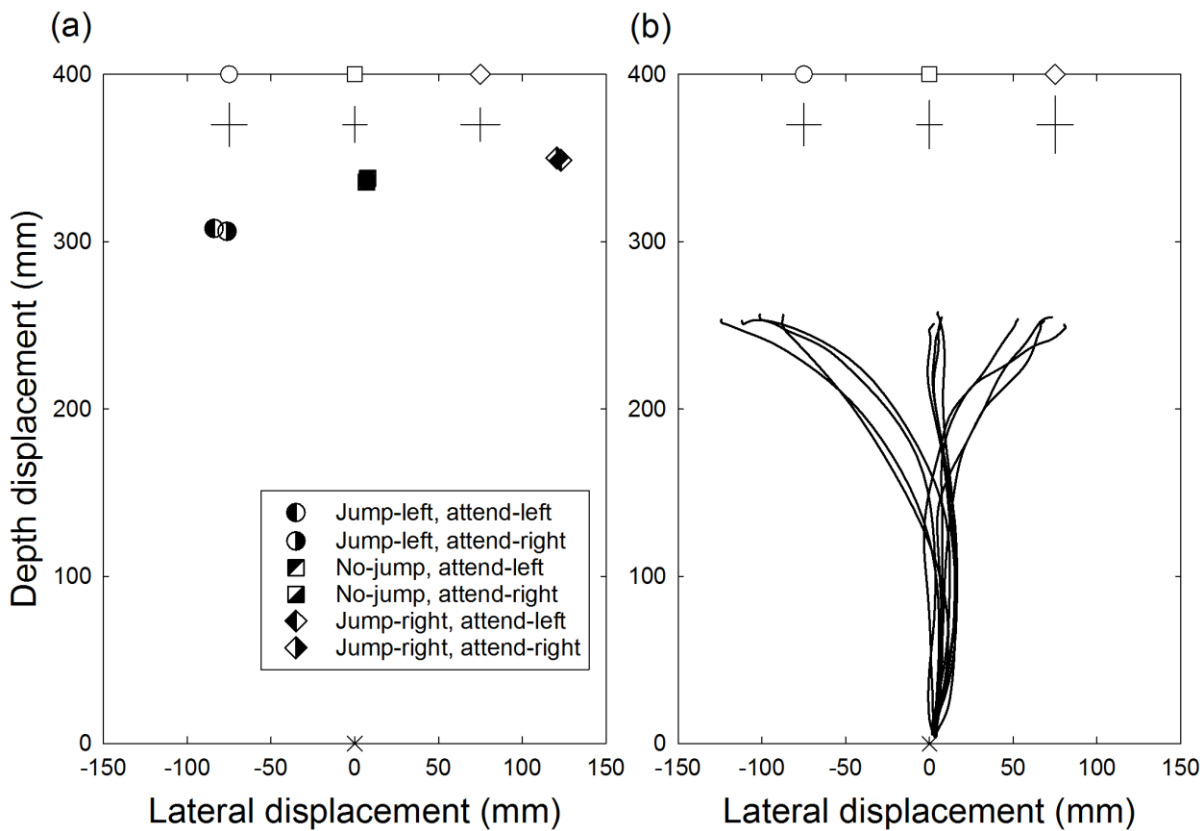


Figure 5.

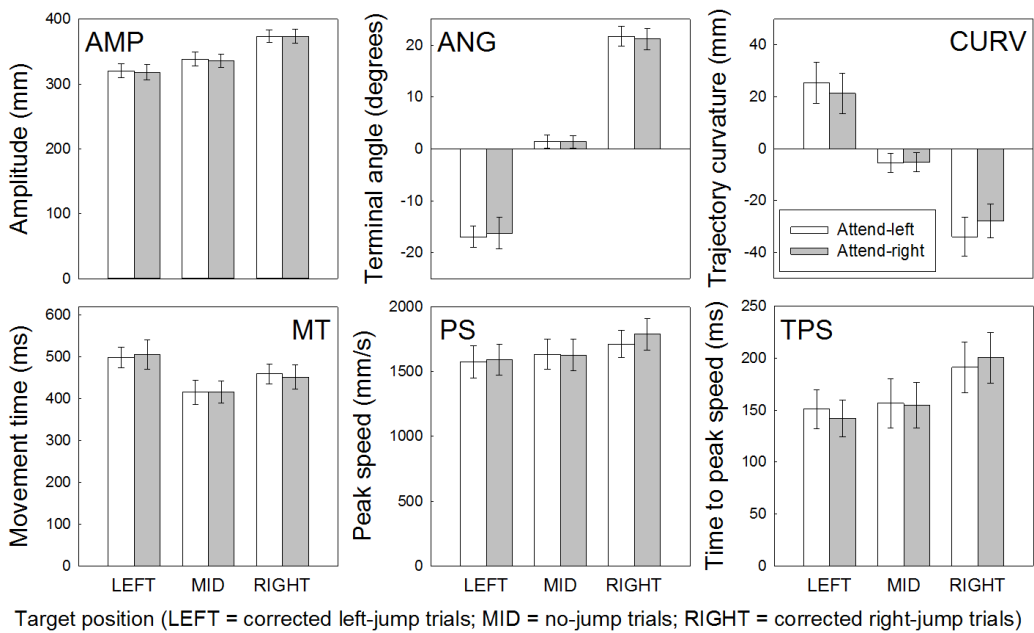


Figure 6.

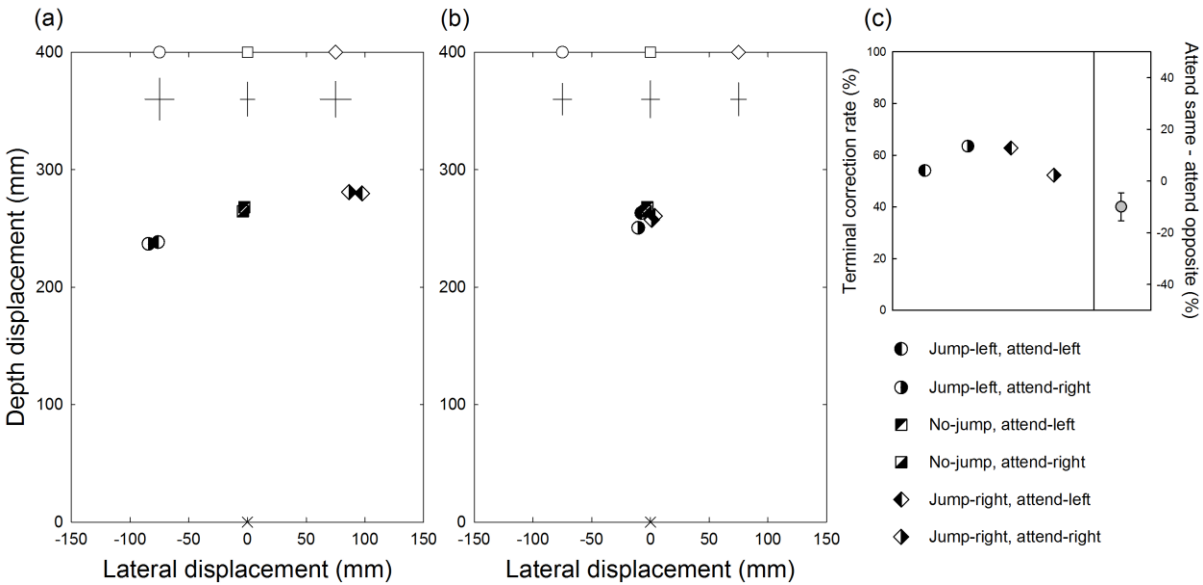


Figure 7.

